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AQUATIC INVERTEBRATE AND VERTEBRATE COMMUNITIES OF EPHEMERAL STREAM ECOSYSTEMS IN THE ARID SOUTHWESTERN UNITED STATES

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ABSTRACT—Ephemeral streams in the southwestern United States have unpredictable, short, torrential flows during extreme weather, and their aquatic biology is poorly studied. During the 2006 monsoon, we sampled aquatic communities at 14 ephemeral stream sites within the Santa Cruz River, Arizona, and Río Puerco, New Mexico, watersheds following a monsoon-related thunderstorm and continuing daily until flows and pools dried. With the 86 taxa of macroinvertebrates that we collected, these sites host a modest community, although presence was limited by drying. Macroinvertebrate taxa richness was not associated with duration of water presence, and biomass was greater in sites with less water available. We collected more taxa in ephemeral reaches of interrupted streams than in truly ephemeral streams. Drought-resistant / resilient species traits were well represented. Vertebrates colonized these ephemeral stream reaches quickly; however, native fish species used ephemeral reaches as corridors between perennial reaches while nonnative fish were unable to do so, and amphibians sometimes completed the aquatic portion of their life cycle in the receding waters. This study provides the first data on aquatic organisms in ephemeral streams immediately after monsoon thunderstorms in the southwestern United States.

RESUMEN—Arroyos efímeros en el suroeste de los Estados Unidos suelen tener flujos impredecibles, breves, y torrenciales durante condiciones meteorológicas extremas, y su biología acuática es poco estudiada. Durante el monzón del 2006, muestreamos las comunidades acuáticas en 14 arroyos efímeros dentro de las cuencas del río Santa Cruz, Arizona, y Río Puerco, Nuevo México, después de una tormenta relacionada con el monzón y continuamos muestreando todos los días hasta que los flujos y charcos se secaron. Con 86 taxa de macroinvertebrados acuáticos, estos arroyos albergaron una comunidad modesta, aunque la presencia fue limitada por la sequía. La riqueza de taxa de macroinvertebrados no se asoció con la duración de la presencia de agua y la biomasa fue mayor en los arroyos con menos agua disponible. Más taxa fueron colectados en secciones efímeras de arroyos interrumpidos que en arroyos verdaderamente efímeros. Características específicas de la resistencia y recuperación a la sequía estuvieron bien representadas. Los vertebrados colonizaron estas secciones efímeras de arroyos rápidamente; sin embargo, especies de peces nativos usaron las secciones efímeras como corredores entre secciones perennes, mientras que los peces no nativos no pudieron hacerlo, y anfibios a veces realizaron la parte acuática de su ciclo de vida en las aguas retrocediendo. Este estudio proporciona los primeros datos sobre los organismos acuáticos en arroyos efímeros inmediatamente después de tormentas monzónicas en el suroeste de los Estados Unidos.

Many studies exist on biota in streams within the arid parts of the western United States; however, the subjects of those studies have mostly been perennial or intermittent summer-dry stream systems, isolated desert potholes, or vernal pools (e.g., Fisher et al., 1982; Grotheer, 1995; Molles, 1985; Del Rosario and Resh, 2000; Lytle, 2000; Lytle et al., 2008; Bogan et al., 2013; Boersma et al., 2014). The biota and succession patterns in ephemeral streams (sensu Armantrout, 1998; Bain and Stevenson, 1999) have not been well studied in the southwestern United States when aquatic habitats are temporarily (e.g., <1 week) created by flow events. The lack of research on truly ephemeral stream channels can be largely attributed to the fact that these stream reaches do not lend themselves well to succession studies, having short, torrential flows during extreme weather and lasting for unpredictable, but generally short, periods thereafter (Williams, 2001).

Because these ephemeral streams represent, for aquatic organisms, a small patch of habitat within an otherwise hostile environment, island biogeographic theories (MacArthur and Wilson, 1967) should apply. These habitats appear suddenly and diminish quickly, and such an environment poses considerable challenges to the organisms that inhabit it (Williams, 2001). Initial and considerable surges of flow power, unpredictable flow permanency, presence/absence of nearby colonization sources, life histories of the colonizing organisms, and stochasticity of colonizer occurrence all should play a role in determining the community in these systems.

Based on previous studies in arid-land streams, the primary species colonizing the small, temporarily wet reaches of ephemeral streams are hypothesized by researchers to be aerial adult colonizers with good powers of dispersal, species with rapid larval development, and those utilizing catastrophic drift from perennial stream reaches upstream (Williams, 2001; Van de Muetter et al., 2007; Lytle and Poff, 2004; Bogan and Boersma, 2012). Migration from nearby sources (e.g., off-channel ponds) is also likely, but probably less efficient, especially for larvae. Migration from the hyporheos is generally not considered to be a valid colonization source for ephemeral stream channels, since the water table is generally quite deep below the streambed; however, aestivating/diapausing life stages within the dry streambed could establish new populations of a few taxa (e.g., *Triops* in ephemeral lentic systems). Fish generally are restricted to drift or migration from downstream or off-channel ponds during overflow conditions (John, 1964; Bêche et al., 2009), while amphibians also generally have terrestrial adults that can aid colonization of a new aquatic resource.

We conducted a natural history study to survey the aquatic macroinvertebrates and vertebrates in several ephemeral streams in two regions in Arizona and New Mexico that flowed for short periods of time after monsoon thunderstorms (AWWQRP, 2006). In part, we made comparisons between sites with upstream perennial refuges of potential colonizers and sites without upstream colonizers, as well as between the two geographic regions. Using these data, we documented succession patterns and tested the hypothesis that greater spatial extent of wetted habitat and longevity of water presence may lead to greater richness of taxa.

MATERIALS AND METHODS—*Study Areas*—Sites were located in one representative watershed each in two broad, geographically diverse regions of the southwestern United States. The two regions contrasted with distinct patterns of precipitation, stream flows, stream substrates, and ecology. We sampled seven sites in the Santa Cruz River watershed near Tucson, Arizona, and seven sites in the Río Puerco watershed northwest of Albuquerque, New Mexico, as described in De Jong and Canton (2014). When we visited all sites in June 2006, they were completely dry, verifying their ephemeral status.

We designated 10 sites as "ephemeral reaches of interrupted streams" because they had perennially flowing reaches farther upstream, while the other four sites were truly "ephemeral streams" (Table 1). The sites that were ephemeral reaches of interrupted streams could have upstream perennial refuges and sources of potential colonizers. We chose sites so that perennial stream reaches in interrupted streams were within 20 km upstream. Because we anticipated that the existence of potential colonization by drift might produce different succession patterns, we analyzed these two types of sites separately.

Methods—Hydrology and Habitat—We identified a U.S. Geological Survey (USGS) gage within each watershed to monitor the development of streamflow: Pantano Wash near Vail, Arizona, (USGS Gage 09484600) and Río Puerco above Arroyo Chico near Guadalupe, New Mexico (USGS Gage 08334000). During late July and early August 2006 (Table 1), we dispatched teams to sample streams after we identified flow-producing precipitation events through online monitoring of the above gages. We began sampling within 24 h after peak flow. We designated a 30–100-m reach at each site and sampled at approximately the same time every day after water started receding from a flash flood. When possible, we also measured the areal extent (in m^2) of water presence within the reach (lotic and lentic) at time of sampling. Due to safety concerns, we could not fully measure all sites during periods of higher flows.

Flows in all sampled streams within the Santa Cruz River watershed ceased within 120 h of peak flow. In some streams, however, new storms and flows happened while we were still in the vicinity, so we continued sampling those sites. Assuming patterns to have been "reset" after drying at these sites (Bogan and Lytle, 2011), we again sampled on those streams 24 h after that subsequent storm (Table 1). In the Río Puerco watershed, flows in all streams continued flowing for 96 to >168 h after peak flow.

Methods—Biotic Sampling—We collected aquatic macroinvertebrate population samples from the designated stream reach at each site on every visit when sufficient water was available. We collected the samples in a manner consistent with the U.S. Environmental Protection Agency's Rapid Bioassessment Protocols for the multihabitat approach (Barbour et al., 1999), with a composite of 20 "jabs" or "kicks" with a modified kick net sampler (500-Im mesh) in all available instream habitats, such as riffles, runs, pools, banks, and snags, regardless of the proportions of habitats available. These protocols generally sampled about 20 m^2 of habitat. As flow decreased or smaller pools were encountered and available habitat could not support the standard effort (e.g., 20 jabs would destructively sample 100% of the habitat), we scaled down our efforts (e.g., 10 jabs or 5 jabs) to sample the available habitat and were documented as such. This happened in only four cases. We preserved samples in 95% ethanol in individual, labeled jars and submitted them to the laboratory.

We collected fish and amphibians using seines, backpack-mounted electrofishing gear, or both to maximize capture probability. We conducted multiple passes using appropriate equipment through available habitat within the designated reach, including open water, scour holes, snags, and submerged vegetation. We measured all areas seined or electrofished for areal extent of sampling effort. We identified all fish and most amphibians, counted them, measured them for length, and, except voucher specimens, released them. We also identified and included in the analyses any incidental captures of amphibian tadpoles in aquatic macroinvertebrate samples.

We sorted all invertebrate samples in their entirety, and identified organisms to the lowest practical taxonomic level where possible (usually genus), depending on the age and

TABLE 1—Schedule of sample collection and day of succession (numbers 1–6) for ephemeral stream systems within the study area, 2006.[a]

Santa Cruz River watershed	29 July	30 July	31 July	1 August	2 August	3 August	4 August	5 August	6 August
Ephemeral reaches of interrupted streams									
Santa Cruz River at Congress	—	↓ H	—	↓ H	↓ 0	1	2	3	D
Pantano Wash at Vail	↓ H	↓ H	↓ H	H	D	D	↓ 0	1	D
Ciénega Creek upstream of I-10	↓ H	—	↓ —	—	2	↓ —	1	2	D
Ciénega Creek downstream of Mescal Arroyo	↓ H	H	↓ 0	1	2	↓ 0	1	2	D
Tanque Verde Wash	—	—	—	↓ 0	D	D	↓ 0	D	D
Ephemeral streams									
Davidson Canyon	↓ 0	1	2	3	D	D	D	D	D
Mescal Arroyo	↓ 0	1	2	3	D	D	D	D	D

Río Puerco watershed	8 August	9 August	10 August	11 August	12 August	13 August	14 August	—	—
Ephemeral reaches of interrupted streams									
Río Puerco near San Luis	↓ 0	1	2	3	4	5	6	—	—
Río Puerco at Cabezón	↓ 0	↓ H	1	2	3	4	5	—	—
Río Puerco downstream of Arroyo Chico	—	↓ —	—	—	3	4	5	—	—
Arroyo Chico upstream of USGS Gage	—	↓ 0	1	2	3	4	5	—	—
Arroyo Chico downstream of USGS Gage	—	↓ —	—	—	3	4	5	—	—
Ephemeral streams									
Cañada Santiago	↓ 0	1	2	3	4	5	6	—	—
Arroyo Balcón	—	↓ 0	1	2	3	4	5	—	—

[a] H = flows too high to sample safely; D = completely dry streambed; — = not sampled; down arrow indicates overnight flow-generating thunderstorm.

condition of the specimen and availability of keys. We mounted chironomid midges and oligochaete worms on microscope slides and identified them to genus under a compound microscope. We measured wet biomass of all collected macroinvertebrates on an AND Corporation GR-202 balance in the laboratory. We identified fish and amphibian voucher specimens and incidental captures to species level in the laboratory. We analyzed by-catch of terrestrial organisms in the invertebrate samples separately in De Jong and Canton (2014).

Data Analysis—Hydrology and Habitat—In addition to monitoring the online hydrographs for the stream gages immediately prior to and during sampling, we used the entire period of record from the two stream gages (1958–2006 for USGS Gage 09484600 and 1943–2006 for USGS Gage 08334000) to analyze normal flow patterns, to identify large flow events preceding our sampling, and to calculate recurrence intervals for the flows we encountered. We calculated recurrence intervals using a log-Pearson Type III regression (Viessman and Lewis, 1996) on annual peak flow data. We plotted areal extent of water presence at each site, normalized to m^2/100-m reach, over time and analyzed data to determine patterns in duration of flow.

Regional and Succession Patterns—To analyze regional biogeographic patterns, we identified the number of distinct taxa across all sites and within each watershed, as well as between the "ephemeral reaches of intermittent streams" and the truly "ephemeral streams," as defined above. We identified which taxa were unique to each watershed and which taxa were most frequently collected.

Because sampling commenced within 24 h after flows began to subside, the days of succession began with day 0 (0–24 hours), then day 1 (24–48 hours), etc. If overnight flow events occurred at a site (based either on online hydrograph data or observations onsite), we assumed the succession patterns to be "reset" to a potentially different trajectory whether or not the site had completely dried (Bogan and Lytle, 2011) and started over at day 0. We used a repeated measures analysis of variance test to determine if significant differences existed in macroinvertebrate taxa richness or biomass of ephemeral reaches of

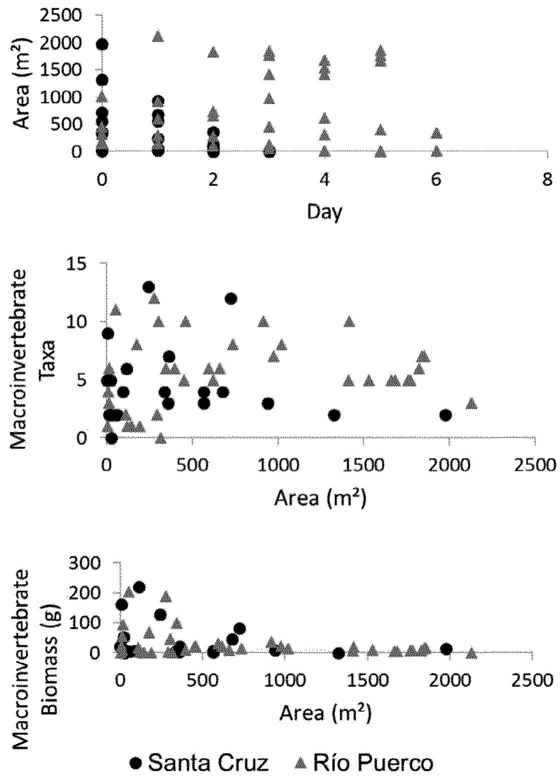

FIG. 1—Plots of habitat available (normalized to area/100-m stream reach) at sites (top), macroinvertebrate taxa richness (middle), and biomass (bottom) in samples collected in streams in the Santa Cruz River, Arizona, and Río Puerco, New Mexico, watersheds, July–August 2006. Samples represented approximately 20 m^2 of habitat within the aquatic habitat available within 100-m stream reach.

intermittent streams between the two watersheds on each of the first four days of succession. We could not test the last three days of succession statistically because the water in each of the Santa Cruz River watershed sites dried up by 96 h after flow began to recede, and we did not test ephemeral streams because there were only two sites per watershed. We plotted number of macroinvertebrate taxa against available habitat (in m^2) to determine if amount of water present may have had an influence on biotic succession patterns, and the patterns had to be evaluated visually instead of statistically because of low number of sites and high variability.

Finally, to determine the potential effect that drought resistance or resilience may have on these early succession patterns, we characterized taxa based on their species traits (Thorp and Covich, 2001; Poff et al., 2006; Boersma et al., 2014). Drought-resistant invertebrates were those with desiccation-resistant life forms (cryptobiota) or an ability to breathe atmospheric oxygen. Drought-resilient invertebrates were those with rapid larval development, female dispersal, and propensity to occur in the drift. However, regardless of resistance or resilience traits, we considered macroinvertebrate taxa with aerial life stages to potentially be the most likely taxa to colonize these ephemeral stream reaches (Williams, 2001; Van de Muetter et al., 2007) and identified them as such. We also identified the primary functional feeding group to which each macroinvertebrate taxon belonged, based on Barbour et al. (1999), to determine patterns of ecological succession.

Because this was primarily a natural history study on this infrequently studied ecosystem, we necessarily kept statistical analysis to a minimum, but any statistics that were performed were conducted in NCSS 2007 (NCSS, LLC, Kaysville, Utah).

RESULTS—Hydrology and Habitat—Average daily discharge values indicate that monsoon flows usually begin at the end of June and continue into late September, with the highest concentration of large rain events occurring in August. In 2006, Tropical Storm Emilia precipitated large rain events in the Santa Cruz River watershed, beginning in the last week of July and continuing into the first week of August. Three large events preceded sampling of the stream communities, and sampling occurred within the receding limb of the event of 31 July. The recurrence interval ranged from 1.75–3.45 years.

The Río Puerco watershed typically has two distinct periods of ephemeral flow. High discharges are first experienced from spring snowmelt in the upper portions of the watershed beginning in late April and extending to late June. A second, higher peak in runoff occurs in response to monsoon events, beginning in July and ending in September, similar to southern Arizona. In 2006, three large flow-producing events began in the first week of August, with biotic sampling beginning on the receding limb of the last (7 August) event. The recurrence interval ranged from 2.30–2.45 years.

Despite the high flows, water levels receded quickly, and all sites were dry again (no surface water) within 9 days following commencement of flow. As noted above, several sites had overnight flow events; however, some of these did not even persist until the site could be sampled the next day. In three instances, connective flows ceased within the arroyos while the research team was on site, leaving only isolated pools for sampling.

The rate of decrease in the amount of aquatic habitat remaining in the streams after the beginning of flow recession varied by watershed, decreasing rapidly in the Santa Cruz River watershed and more slowly in the Río Puerco watershed (Fig. 1, top). As flows and amount of aquatic habitat decreased in both watersheds, we generally saw little change in the number of aquatic macroinvertebrate taxa utilizing the sampled habitat (Fig. 1, middle), but an increase in biomass (Figure 1, bottom).

Biotic Sampling—We collected a total of 86 distinct taxa of aquatic macroinvertebrates (Appendix 1), including representatives of the Insecta, Hydracarina, Crustacea, Oligochaeta, Hirudinea, and Gastropoda. Insects were the most diverse group, with 74 distinct taxa, including Collembola, Ephemeroptera, Odonata, Hemiptera, Coleoptera, and Diptera. Most of the insect taxa (82.6%) had aerially dispersing adults. Functional feeding groups represented in the dataset included filter-collectors (3 taxa), gatherer-collectors (28 taxa), plant-piercers (6 taxa), predators (41 taxa), scrapers (4 taxa), and shredders (4 taxa).

In the Santa Cruz River watershed, we collected 44 distinct taxa of aquatic macroinvertebrates. Average taxon richness per site was 9 taxa, ranging from 3–21 taxa. We found fewer taxa at sites where flows following flood events were reduced quickly to isolated pools than at sites in which water continued flowing, and also found fewer taxa at sites where samples were taken infrequently because flows were either too high or nonexistent than at sites where water was present more consistently. We collected 33 taxa at only a single site in the Santa Cruz River watershed, 7 taxa were collected at 2 sites, and 3 taxa were collected at 3 sites. Very immature unidentified Orthocladiinae (possibly representing numerous species) were found at six of the seven sites in the watershed.

We collected 63 distinct taxa of aquatic macroinvertebrates in the Río Puerco watershed. Average taxon richness per site was 19 taxa, ranging from 5–32 taxa. As in the Santa Cruz River watershed, we found fewer taxa at sites in which postflood flows were quickly reduced to isolated pools than at sites in which water was still flowing when we sampled. We found 31 taxa only at 1 site, with 12 taxa collected at 2 sites, 11 taxa collected at 3 sites, and 6 taxa collected at 4 sites. We found adults of the genus *Ochthebius*, a hydraenid beetle, at five of the seven sites, and unidentified, immature baetid mayflies at six of the seven sites. There were no statistically significant differences in invertebrate taxa richness between the Santa Cruz River and Río Puerco watershed sites for days 0–3 in ephemeral reaches of interrupted streams ($F_{1,23} = 0.06$, $P = 0.808$). Likewise, biomass was not significantly different between the two watersheds ($F_{1,23} = 0.45$, $P = 0.507$).

In sites with known or likely upstream sources of potential colonizers, we collected 77 aquatic macroinvertebrate taxa in the 7-day succession period (Appendix 1). Within the first 24 h (day 0), we collected 33 taxa of aquatic macroinvertebrates in these streams. Taxon richness decreased over time, with only 6 taxa collected on day 5. We collected dryopid beetles in the genus *Postelichus* and unidentified Orthocladiinae (potentially comprising multiple taxa) on every day of succession. We collected other taxa on both day 0 and day 6, suggesting that they could possibly be present throughout succession; these taxa included the mayflies in the genus *Callibaetis*, damselflies that were either *Coenagrion* or *Enallagma*, and immature waterboatmen (Corixidae). Eight of the 33 taxa that we collected within the first 24 h were not collected on later days.

Conversely, we collected 35 aquatic macroinvertebrate taxa within the 7-day succession period on these streams with no known upstream source of potential colonizers (Appendix 2). Within the first 24 h (day 0), 4 taxa of aquatic macroinvertebrates were collected in these streams, and only 1 of those taxa (an unidentified Tipulidae) was not collected again during the course of the study. We collected unidentified Orthocladiinae every day through day 4, and we collected the leech *Erpobdella punctata*, the hydraenid beetle *Ochthebius*, and the midge *Procladius* every day from day 2 to the end of the study. This aspect of the study was constrained by the fact that less than a third of the streams studied were truly ephemeral streams, so the lower number of taxa is not surprising.

We collected four species of fish: green sunfish (*Lepomis cyanellus*), longfin dace (*Agosia chrysogaster*), fathead minnow (*Pimephales promelas*), and western mosquitofish (*Gambusia affinis*). We found longfin dace in one site in the Santa Cruz River watershed; we found fathead minnows in three sites in the Río Puerco watershed. We found the nonnative green sunfish and western mosquitofish in one site in the Santa Cruz River watershed. We also collected five species of amphibians in the Santa Cruz River and Río Puerco watersheds: American bullfrog (*Rana catesbeiana*), Couch's spadefoot toad (*Scaphiopus couchi*), prairie spadefoot toad (*Spea bombifrons*), red-spotted toad (*Anaxyrus punctatus*), and an unidentified *Bufo*. We found Couch's spadefoot toads and red-spotted toads at four sites, distributed across both watersheds. The prairie spadefoot toad and unidentified *Bufo* were each at one site in the Río Puerco watershed. We found two dead bullfrogs at one site in the Santa Cruz River watershed. With the exception of the bullfrogs and one Couch's spadefoot toad, all amphibians collected were tadpoles.

Discussion—Hydrology and Habitat—Recurrence intervals of these flows ranged from 1.75–3.45 years, slightly greater than the effective discharge recurrence interval of 1.15–1.40 years for Southwestern streams (Graf, 2002). This indicates that these events, while appearing large, were not unusual, and our observations on the aquatic biology would be fairly representative of normal circumstances.

A likely reason behind the differences in rates of habitat loss between the two watersheds could be the types of sediment present in the channels and stream banks. In the Santa Cruz River watershed sites, the primary substrate and source material in the banks was large-grained sand. This appeared to allow rapid penetration of water into the stream bottom, resulting in loss of surface flow rapidly following cessation of rain. Conversely, in the Río Puerco watershed sites, the primary substrate was fine silts and clays, which appeared to "seal" the stream bottom, precluding rapid penetration of the water into the stream bottom. Furthermore, we observed that the banks in the Río Puerco watershed retained water much longer than the coarse sand soils in the Santa Cruz River watershed, releasing it slowly over time into the channel, actually adding slightly to the flows and making additional aquatic habitat available. A second possible reason for the greater available habitat in the Río Puerco sites might have been continued light rainfall in the headwaters of that watershed at the time of sampling, although it is unclear if those waters ever flowed all the way to our sites.

The lack of change in the number of taxa utilizing available habitat and increasing biomass as habitat decreased is in contrast to other studies, such as that of Graham (2002), which found positive correlations between invertebrate taxa richness and available aquatic habitat in ephemeral pools in Wupatki National Monument, Arizona, and conceptual models in Williams (1977) and Bogan et al. (2013). The reason could lie in the extremely short ephemeral nature of these patches and the time frame of the study (ffi9 days), not allowing an equilibrium community to form (Hutchinson, 1951, 1953) or that the contraction in available habitat concentrated the invertebrates. These organisms are likely adapted to rapid growth, so the increase in biomass over time is not surprising.

Macroinvertebrates—Ephemeral Reaches of Interrupted Streams—Most (84%) of the aquatic macroinvertebrate taxa collected in ephemeral reaches of interrupted streams had aerially dispersing life stages (Appendix 1), illustrating the importance of this life history trait. Nearly a third of these taxa (32%) were present in the aerial stage (usually beetles) and represented the majority of the drought-resistant forms, but the rest were generally found in the samples as small, immature larvae, such as would be expected from recently laid and hatched eggs. When aerial taxa were present, but the aerial life stage was not present, drought-resilient taxa were better represented than drought-resistant taxa. A few taxa were represented by older larvae, which apparently arrived from upstream sources. These taxa included the mayfly genus *Callibaetis*, the predaceous midge genus *Chaoborus*, and the hydrophilid beetle genus *Berosus*. Additionally, *Chaoborus* is primarily a lentic form, being found in lakes and ponds and rarely in flowing water (Cook, 1956), suggesting it could have been washed into the stream from off-channel ponds or permanent isolated in-channel pools upstream, rather than intermittent flowing sections of the stream.

The remaining 12 taxa collected in ephemeral reaches of interrupted streams did not have aerially dispersing life stages (Thorp and Covich, 2001). Although these taxa could have come from upstream perennial water sources, they also could have come from other sources, such as cryptobiotic states (e.g., the tadpole shrimp genus *Triops*) or the hyporheic zone, or as transients on birds and other wildlife (e.g., the leech *E. punctata* and the snail genus *Helisoma*) Conversely, some taxa, such as the Collembola and the enchytraeid worms, also could have been terrestrial forms, misinterpreted as aquatic forms, which were incidentally collected in the samples. *Hyalella azteca* were almost certainly from upstream sources, given their limited vagility.

Most colonizing taxa were predators and gatherer-collectors, with new taxa from these groups arriving each day. Eighty percent of the piercer taxa arrived on day 0, and these were highly vagile taxa such as corixids (plant-piercers) and naucorids (predator-piercers). It did not appear that functional feeding group membership greatly affected the order of succession pattern in these streams.

Macroinvertebrates—Ephemeral Streams—Similar to the streams with upstream sources of potential colonizers, however, most (83%) of the aquatic macroinvertebrate taxa in the streams without upstream sources had aerially dispersing life stages. Nearly half of these (45%) were present in their aerial form, again also representing most of the drought-resistant forms, but, somewhat surprisingly, they did not arrive until day 2 of succession. The rest of the aerial taxa were represented by small, immature larvae. As expected, it was not until day 2 of succession (72 h after flows began to subside) that taxa without aerially dispersing life stages were collected. These six taxa included the tadpole shrimp in the genus *Triops*, three taxa of annelid worms, the leech *E. punctata*, and the snail genus *Stagnicola*. Because these streams did not have known upstream sources of potential colonizers, as discussed above, they might have been terrestrial representatives of these groups (misinterpreted as aquatic forms, e.g., worms in the families Enchytraeidae and Lumbriculidae), organisms in cryptobiotic states (e.g., *Triops*), hyporheic organisms, or transients on wildlife (leeches and snails). *Hyalella azteca* was not collected in these streams.

As in the ephemeral reaches of interrupted streams, these streams were dominated by predators and gatherer-collectors. Three of the four taxa that arrived on day 0 were gatherer-collectors, with most of the gatherer-collector taxa arriving first on day 2; however, gatherer-collector taxa were not collected after day 4. Predators did not arrive until day 2, but additional predator taxa arrived on days 3, 4, and 5. All three taxa that were present from day 2 to the end of the study were predators. It appears that there may have been some potential patterns in the role of functional feeding groups in succession patterns, but this is certainly fodder for further study.

Vertebrates—Fish were generally obligated to rely on upstream sources for colonization. Longfin dace were found only on day 1 of succession and only in Ciénega Creek. Longfin dace are adapted to take advantage of flash floods for downstream dispersal, entering the flow when it starts and being carried downstream to other perennial reaches for colonization (Minckley, 1973). If flows do not transport them to suitable habitat, they are also known to burrow under logs, stones, and algal mats in wet sand to await another high flow event. We observed this species burrowing in loose sand as we tried to collect them in Ciénega Creek. After flows disappeared, we looked in wet sand and mud under rocks and vegetation mats to determine if this behavior was occurring elsewhere in the study streams, but we were unable to locate any fish. These data indicate that longfin dace can be present in ephemeral stream ecosystems within 1 day after flows begin to subside, but apparently are transient and do not persist in these ephemeral reaches.

Fathead minnows can be present in these ephemeral stream ecosystems within 3–5 days after high flows begin to subside, we collected them on day 3 in Cañada Santiago and on day 5 in the Río Puerco at San Luis and the Arroyo Chico upstream of the USGS gage. Both of the tributary sites were located immediately above their confluences with the Río Puerco, which had a known upstream source of fathead minnows at the town of Cuba, so they could have dispersed into the sites from downstream as flows began to slowly recede. This is consistent with collections delayed 3–5 days after flows begin to recede. Fathead minnows do not appear to have similar survival strategies as the longfin dace, but rather rely on high reproductive rates and tolerance of extreme conditions for survival (Minckley, 1973). Since flows had not fully disappeared by the cessation of sampling in the Río Puerco, we do not know how long these fish would have persisted.

We found green sunfish and mosquitofish only as dried specimens in the middle of the dry streambed in Tanque Verde Wash after flows disappeared. Reduced flows and disappearance of available habitat had a substantial impact on these nonnative species, which likely came from an off-channel pond, which are numerous along Tanque Verde Wash.

We found bullfrogs and red-spotted toads on day 0 of succession, and found red-spotted toads on every day of succession through day 5. We did not observe or collect either species of spadefoot toad until day 4 of succession. Since most adult amphibians are terrestrial, they do not require an upstream source population to potentially colonize a stream segment. These data indicate that amphibians can be present in these ephemeral stream ecosystems almost as soon as high flows begin to subside, and they remain in the streams until adulthood if surface water persists. The adult stage of the life cycle of most of the amphibian species we collected is well able to survive without pools or streams, but the other life stages require water. Several populations of amphibians enjoyed sufficient duration of flow that they would have survived to adulthood, since some toads collected in the Río Puerco watershed sites were already beginning to metamorphose into adults by the end of the sampling effort. On a few occasions, however, we observed dead tadpoles being scavenged by ants in pools that had dried, such as in Mescal Arroyo, Arizona.

We did not observe the complete termination of flow in the Río Puerco watershed, but there was no surface water remaining at any of the sites in the Santa Cruz River watershed on the last day of sampling. As expected, there were no aquatic organisms remaining alive at the dry sites—except possibly those that had entered cryptobiotic life stages and were distributed in the dry sediment. Although it is possible that some aquatic organisms might have burrowed into the substrate to use the hyporheic zone as a refugium (Williams, 1984; Williams and Hynes, 1976), this does not always happen (Del Rosario and Resh, 2000), since the water table in these streams is likely too low for them to reach effectively.

Conclusions—These results describe the aquatic community that can quickly colonize ephemeral streams in the arid southwestern United States. These waters appear capable of supporting a relatively diverse assemblage across the short time frame during which they flow. As expected from island biogeography theory, nearby (in this case, upstream) sources of potential colonizers appear to be important for the formation of both invertebrate and vertebrate communities in these ephemeral streams. However, upstream sources are not required for the invertebrate communities, since the primary source of colonization for the insects is the aerial adult stage. Drought-resilient forms are more prevalent when the aerial stage of aerially dispersing invertebrates is not present. Cryptobiotic life stages might also form sources for colonizers among some species. Amphibians can colonize from terrestrial adults. Functional feeding group membership did not appear to influence the order of aquatic invertebrate succession in these streams.

Overall, there was only a hint of change in the benthic invertebrate communities once succession began, with a rather strong signal of opportunistic colonization. This is interesting in light of the conceptual models of Williams (1977) and Bogan et al. (2013), and could be due to the short time frame for this study (ffi9 days). Finally, a fundamental characteristic of these ephemeral stream ecosystems is that they are present for an unpredictable, short period of time, which places considerable time constraints on the survival of any organisms, invertebrate or vertebrate, that choose to inhabit these waters.

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Appendix 1—Succession of macroinvertebrate taxa in ephemeral reaches of interrupted streams[a] in the study area, July–August 2006, sorted first by presence of aerially dispersing life stages, then by day of succession. Day of succession based on hours after flash flood waters began to recede (e.g., day 0 = 0–24 h).

	Ecological traits				Day of succession						
Taxon	Drought resistant	Drought resilient	Aerial dispersal[b]	FFG[c]	0	1	2	3	4	5	6
Unidentified Orthocladiinae		X	X	GC	X	X	X	X	X	X	X
Chironomus		X	X	GC	X	X	X	X	X		
Berosus	X		X	PI	X	X			X	X	
Chaoborus			X	PR	X	X					
Ormosia			X	GC	X	X					
Unidentified Salpingidae			X	PR	X		X	X	X		
Unidentified Tipulidae			X	SH	X		X	X	X		
Unidentified Ceratopogoninae		X	X	PR	X		X	X		X	
Unidentified Culicidae		X	X	FC	X		X	X			
Unidentified Dolichopodidae			X	PR	X		X				
Unidentified Corixidae	X		X	PI	X			X	X		X
Unidentified Ceonagrionidae			X	PR	X			X		X	
Callibaetis		X	X	GC	X			X			X
Coenagrion/Enallagma			X	PR	X				X		X
Lipogomphus			X	PR	X				X		
Tabanus	X		X	PR	X					X	
Apedilum		X	X	GC	X						
Unidentified Muscidae			X	PR	X						
Pseudosmittia		X	X	GC	X						
Stratiomys	X		X	FG	X						
Unidentified Veliidae	X		X	PR	X						
Unidentified Baetidae		X	X	GC		X	X	X	X	X	
Bryophaenocladius		X	X	GC		X	X	X	X		
Goeldichironomus		X	X	GC		X	X	X			
Unidentified Ephydridae		X	X	GC		X	X				
Unidentified Empididae			X	PR		X		X			
Unidentified Chironomidae		X	X	GC		X					
Unidentified Dytiscidae	X		X	PR		X					
Smittia		X	X	GC		X					
Unidentified Syrphidae	X		X	GC		X					
Unidentified Notonectidae	X		X	PR			X		X		
Nemotelus		X	X	GC			X				
Conchapelopia/ Thienemannimyia		X	X	PR				X	X		
Endotribelos		X	X	GC				X		X	
Unidentified Libellulidae			X	PR				X			
Paramerina		X	X	PR				X			
Procladius		X	X	PR				X			
Rheumatobates	X		X	PR					X		
Unidentified Gerridae	X		X	PR						X	
Larsia		X	X	PR						X	
Polypedilum		X	X	SH						X	
Stictochironomus		X	X	GC						X	
Postelichus	X		XX	SC	X	X	X	X	X	X	X
Laccophilus maculosus	X		XX	PR	X	X	X				
Peltodytes	X		XX	PI	X	X	X				
Belostoma	X		XX	PR	X	X					
Boreonectes striatellus	X		XX	PR	X		X	X	X	X	
Corisella	X		XX	PR	X			X			
Eretes occidentalis	X		XX	PR	X						
Hesperocorixa	X		XX	PI	X						
Microcylloepus pusillus	X		XX	GC	X						
Liodessus obscurellus	X		XX	PR		X	X	X			
Sigara	X		XX	PI		X	X	X			
Enochrus	X		XX	GC		X		X			

APPENDIX 1—Continued.

Taxon	Ecological traits				Day of succession						
	Drought resistant	Drought resilient	Aerial dispersal[b]	FFG[c]	0	1	2	3	4	5	6
Aquarius	X		XX	PR		X					
Hydrochus	X		XX	SH		X					
Ochthebius	X		XX	PR			X	X	X		
Laccophilus	X		XX	PR			X	X			
Microvelia	X		XX	PR			X				
Helichus	X		XX	SC				X	X		
Ambrysus mormon	X		XX	PR				X		X	
Neoporus dimidiatus	X		XX	PR					X		
Oreodytes	X		XX	PR					X		
Unidentified Lumbriculidae				GC	X	X	X	X	X	X	
Hyalella azteca				GC	X	X	X	X		X	
Unidentified Megadrili				GC	X	X	X			X	
Erpobdella punctata				PR		X	X	X			
Unidentified Enchytraeidae				GC		X		X	X		
Hydryphantes				PR		X					
Unidentified Collembola				GC			X				
Unidentified Tubificidae				GC				X	X		X
Triops	X			GC				X		X	
Unidentified Sminthuridae				GC				X			
Helisoma				SC					X		
Tyrellia				PR						X	

[a] Streams include Pantano Wash at Vail, Ciénega Creek upstream of I-10, Ciénega Creek at Mescal Arroyo, Tanque Verde Wash at Houghton Road, and Santa Cruz River at Congress in the Santa Cruz River watershed, and Arroyo Chico upstream of USGS Gage, Arroyo Chico downstream of USGS Gage, Río Puerco near San Luis, Río Puerco at Cabezón, and Río Puerco Downstream of Arroyo Chico in the Río Puerco watershed.

[b] Aerial dispersal: X = taxon has an aerially dispersing life stage; XX = taxon was present in the aerially dispersing life stage.

[c] FFG = Functional feeding groups; FC = filter-collector; GC = gatherer-collector; PI = piercer; PR = predator; SC = scraper; SH = shredder.

APPENDIX 2—Succession of macroinvertebrate taxa in ephemeral streams[a] in the study area, July–August 2006, sorted first by presence of aerially dispersing life stages, then by day of succession. Day of succession based on hours after flash flood waters began to recede (e.g., day 0 = 0–24 h).

	Ecological traits				Day of succession						
Taxon	Drought resistant	Drought resilient	Aerial dispersal[b]	FFG[c]	0	1	2	3	4	5	6
Unidentified Orthocladiinae		X	X	GC	X	X	X	X	X		
Unidentified Ephydridae		X	X	GC	X	X	X	X			
Aedes		X	X	GC	X		X				
Unidentified Tipulidae			X	SH	X						
Unidentified Culicidae		X	X	FC		X			X		
Procladius		X	X	PR			X	X	X	X	X
Psorophora		X	X	FC			X	X			
Bryophaenocladius		X	X	GC			X	X			
Smittia		X	X	GC			X				
Berosus	X		X	PI			X				
Unidentified Salpingidae			X	PR			X				
Tabanus	X		X	PR			X				
Unidentified Baetidae		X	X	GC				X	X		
Unidentified Ceratopogoninae		X	X	PR				X		X	
Unidentified Empididae		X	X	PR				X			
Unidentified Coenagrionidae			X	PR					X		X
Ochthebius	X		XX	PR			X	X	X	X	X
Sigara	X		XX	PI			X	X	X		
Notonecta	X		XX	PR			X				
Agabus	X		XX	PR			X				
Neoporus dimidiatus	X		XX	PR			X				
Paracymus	X		XX	PR			X				
Helophorus	X		XX	SH			X				
Enochrus	X		XX	GC				X			
Laccobius	X		XX	PI				X			
Tropisternus	X		XX	PR				X			
Lipogomphus			XX	PR					X	X	
Liodessus obscurellus	X		XX	PR					X		
Ambrysus mormon	X		XX	PR						X	
Erpobdella punctata				PR			X	X	X	X	X
Unidentified Enchytraeidae				GC			X	X			
Eubranchipus				GC			X	X			
Unidentified Lumbriculidae				GC			X	X			
Stagnicola				SC			X	X			
Unidentified Megadrili				GC			X		X		

[a] Streams include Mescal Arroyo at Marsh Station Road and Davidson Canyon at Mesquite Mesa Road in the Santa Cruz River watershed, and Arroyo Balcón and Cañada Santiago in the Río Puerco watershed.

[b] Aerial dispersal: X = taxon has an aerially dispersing life stage; XX = taxon was present in the aerially dispersing life stage.

[c] FFG = Functional feeding groups; FC = filter-collector; GC = gatherer-collector; PI = piercer; PR = predator; SC = scraper; SH = shredder.